Soil Tillage and Epigeal Predatory Arthropods

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CONTENTS

11.1 INTRODUCTION

There are good reasons to adopt farming practices that promote the activity, abundance, and species diversity of the epigeal community of predatory arthropods commonly associated with arable fields. Many of these animals are natural enemies of crop pests, and the potential of some taxa (e.g., carabid beetles, staphylinid beetles and spiders) to suppress pest populations and reduce the impact of pests on crop production are well documented.[1–11] The enhancement of such beneficial fauna may allow considerable reduction in the use of pesticides, leading to reduced farm costs and less environmental pollution.

Although the importance of predatory arthropods as natural enemies in sustainable agriculture is widely accepted, in general their population dynamics are poorly understood in relation to the overall dynamic complexity of the agricultural landscape itself. For example, field management practices such as soil tillage, weed control, pesticide use, fertilization, harvesting, and the rotation of crops can impose a continuous sequence of habitat disturbances that frequently interact and impinge on the localized survival of natural enemy populations.[5,8,12,13] Furthermore, since many predator species are highly dispersive[14–17] and may require, or utilize in an opportunistic way, the resources of different farmland habitats for feeding, reproduction, and overwintering at certain stages during their life cycle,[18–30] population processes within a particular field can be influenced by the management of surrounding crops and of neighboring uncultivated areas, such as field margins, hedgerows, and woodland, at the broader spatial scale of the whole farm or landscape in which the field is located.[14,31–38]

This chapter examines one aspect of crop management—the way in which different tillage systems, either directly or indirectly, influence the population dynamics of epigeal predatory arthropods; but in view of the many possible spatiotemporal interactions outlined above, these effects are considered in the context of other agricultural practices at the field, farm, and landscape level. It aims to show how tillage systems might be modified or adjusted to enhance or maintain indigenous populations and communities of predatory arthropods in order to maximize the natural regulation of crop pests in the long term.

However, before dealing with this issue it is essential to review the diversity of epigeal predatory arthropods inhabiting arable land, their potential value as natural enemies of crop pests, and their ability to suppress pest populations and reduce pest damage.

11.2 PREDATORY ARTHROPODS IN ARABLE CROPS

Several hundred species of epigeal predatory arthropods have been recorded in arable crops. Most are spiders (Araneae) belonging to the families Linyphiidae, Lycosidae, Clubionidae, and Tetragnathidae, or beetles (Coleoptera) of the families Carabidae Staphylinidae, Cantharidae, and Coccinellidae. Other taxa that are sometimes fairly numerous include predatory mites (Acari), harvestmen (Opiliones), earwigs (Dermaptera: Forficulidae), bugs (Heteroptera: e.g., some Anthocoridae, Miridae, and Nabidae), lacewings (Neuroptera: Chrysopidae and Hemerobiidae), flies (Diptera: e.g., some Asilidae, Empididae, Dolichopididae, Scathophagidae, and Syrphidae), ants (Hymenoptera: Formicidae), and centipedes (Chilopoda).

Comparable surveys of arable fields in Austria,[28] Belgium,[39,40] Britain,[41–46] France,[47] Germany,[48,49] the Netherlands,[50] Poland,[51] Sweden,[52,53] and Switzerland,[54,55] suggest that this range of predatory fauna is very typical of arable land throughout most of Europe. Similar diverse epigeal communities of predatory arthropods are reported from arable crops in parts of Asia[56–58] and North America.[59–66] A large number of species, particularly among the predatory beetles and spiders, appear to be widespread over fairly large geographical areas,[9,64,67,68] and the same predator

species (or close taxonomic and ecological homologs) often occur in many different crop types such as grassland, cereals, brassicas, legumes, root crops, lettuce, strawberries, other vegetables, and soft fruits.[12,50,59,64,68–73]

11.2.1 Predation on Crop Pests

Some epigeal predatory arthropods are specialist feeders, e.g., the so-called aphidophagous or "aphid-specific" Neuroptera, Coccinellidae, and Syrphidae,[74–76] but the vast majority are more or less polyphagous and appear to feed indiscriminately on a wide range of invertebrate prey species.[5,8,9,54,55,68,77–84] The term "polyphagous," as used here and in much of the literature on integrated farming and pest management, is somewhat misleading since many of the epigeal arthropods classed as generalist predators (in contrast to the recognized aphidophagous taxa mentioned above) are perhaps better regarded as stenophagous species with varying degrees of dietary specialization.[78,81,82] The predominance of particular prey items in the diet of some taxa may reflect morphological adaptations, such as the extensible mouthparts of *Stenus* spp. (Staphylinidae), the setal "cages" on the head and antennae of *Leistus* and *Loricera* spp. (Carabidae), which are thought to facilitate capture of springtails (Collembola),[85,86] and the very narrow head and thorax of cychrine Carabidae, which appear to be adaptations for feeding on shell-bearing Mollusca, allowing these beetles to enter snail shells and reach the soft body parts inside;[86] but, probably the main factor giving rise to a stenophagous feeding habit among predatory arthropods is the availability of prey. This may be restricted due to the particular habitat niche in which the predator normally lives[82,87] or limited by body size where the predator may be either too small or too large to handle certain items of prey.[82,88] Nevertheless, while accepting that stenophagy is probably widespread, throughout this account all epigeal predatory arthropods, with the exception of aphidophagous Neuroptera, Coccinellidae, and Syrphidae, are broadly grouped as polyphagous (or generalist) feeders.

Reported findings from laboratory feeding tests, field observations, and the analysis of gut contents show that many of the common polyphagous predators inhabiting arable fields are opportunistic feeders on the various developmental stages of important crop pests, such as aphids and other Homoptera; the caterpillars of some butterflies, moths, and sawflies; the eggs, larvae, and adults of several root- and stem-mining Diptera and leaf-feeding Coleoptera; as well as various species of slugs and snails. The many records from Europe, Asia, North America, and elsewhere of predation on key groups of arable pests are summarized in Table 11.1. The insect polyphagous predators known to attack pests of wheat, cotton, and lucerne in parts of North America are catalogued by Frank and Slosser,[64] and records of predation by spiders on agricultural pests all over the world are reviewed by Riechert[5] and Nyffeler and Benz.[9]

The epigeal predatory faunas of most arable fields are largely dominated by taxa generally considered "ground-dwellers" (e.g., most of the Carabidae, Staphylinidae, Lycosidae, and the erigonid Linyphiidae); in fact, many such species are known to forage in search of prey both on the soil surface and by climbing into the crop canopy. For example, laboratory observations suggest that the carabid, *Agonum dorsale*,

Table 11.1 Reported Predation by Polyphagous Epigeal Arthropods (i.e., Excluding "Aphid-Specific" Neuroptera, Coccinellidae and Syrphidae) on Various Invertebrate Pests of Arable Crops

PREDATOR TAXON (*c*. Number of Species)	Cereal aphids	Rice leafhoppers	Potato aphids	Sugarbeet aphids	Cabbage aphids	Legume aphids	Other Homoptera	Cereal frit fly	Wheat bulb fly	Wheat blossom midges	Cabbage root fly	Carrot fly	Crane flies	Other Diptera	Noctuid moths	Pierid butterflies	Other Lepidoptera	Cereal leaf beetle	Corn rootworm beetle	Colorado potato beetle	Wireworm/Chafer beetles	Other Coleoptera	Sawflies	Slugs & snails
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
COL.: CANTHARIDAE																								
Cantharidae larvae indet.	●																							
Cantharis (4)	●			●																				
Malthinus (1)	●																							
Podabrus (1)							●														●			
Rhagonycha (2)	●																							
COL.: CARABIDAE																								
Abax (1)																								
Acupalpus (1)											○													
Agonum (= *Platynus*) (4)	●			○	○		●	●	○	●	●				○	●			○		●			
Amara (17)	●			○				○	○	●	●			●	●	●					●			●
Anisodactylus (1)																						○		
Asaphidion (1)	●										●													
Bembidion (14)	●			○				○	○	●	●	○		○	○				○			○	○	
Bradycellus (1)									○		○													
Broscus (2)															●					○				
Calathus (3)	●										●													
Callida (2)							●								●									

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Calosoma (4)														●	●			○				
Carabidae adults indet.																						
Carabidae larvae indet.																						
Carabus (10)														●			○	●				
Chlaenius (3)																						
Clivina (1)	●		○					○		●							○		●	○		
Cratacanthus (1)																				○		
Ctenognathus (1)																						●
Cyclotrachelus (1)																					○	
Cychrus (1)																						●
Demetrias (= *Risophilus*) (1)	●							○		○												
Dolichus (1)															○			○				
Dromius (1)	●																					
Evarthrus (1)														○			○			○		
Harpalus (= *Ophonus*) (7)	●	○	●			●	○	○	○	●				●	●		○	○	●	○	○	●
Holcaspis (1)																						●
Lebia (2)																			●			
Loricera (1)	●						○	○	○													
Megacephala (2)																						
Metaglymma (1)															●							
Nebria (1)	●						○	○		●												
Notiophilus (1)	●						○	○														
Odacantha (1)														●								
Olisthopus (1)										○												
Ophionia (1)												○				●						
Patrobus (1)			○																			
Plocamostethus (1)																						●
Pterostichus (= *Poecilus*) (14)	●		●	○		●	●	○	○	●		○		●	●		○	●	●	○	○	●
Scaphinotus (1)																						●
Scarites (2)														○			○			○		
Synuchus (1)	●									○												
Tachys (1)																		○				

(*Continued*)

Table 11.1 (**Continued**)

PREDATOR TAXON (c. Number of Species)	PESTS																							
	Homoptera							Diptera							Lepid.			Coleoptera						
	Cereal aphids	Rice leafhoppers	Potato aphids	Sugarbeet aphids	Cabbage aphids	Legume aphids	Other Homoptera	Cereal frit fly	Wheat bulb fly	Wheat blossom midges	Cabbage root fly	Carrot fly	Crane flies	Other Diptera	Noctuid moths	Pierid butterflies	Other Lepidoptera	Cereal leaf beetle	Corn rootworm beetle	Colorado potato beetle	Wireworm/Chafer beetles	Other Coleoptera	Sawflies	Slugs & snails
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Trechus (3)	●			○			●	●	○	○	●	●				●			○					
Trichocellus (1)															○									
COL.: MELYRIDAE																								
Collops (1)																				●				
COL.: STAPHYLINIDAE																								
Aleochara (4)							●		●		●	●		●							○			
Aloconota (1)	○																							
Anotylus (1)	○										●													
Apocellus (1)																					○			
Atheta (= *Aloconota*) (1)	○						●																	
Leptacinus (1)															○									
Metaxya (1)												○												
Neohypnus (1)																					○			
Ocypus (= *Staphylinus*) (2)																								●
Oxytelus (1)							●				●													
Paederus (2)	●						●													●				
Philonthus (7)	●								○		●				○									
Quedius (1)																								●

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Rugilus (1)	●																									
Staphylinidae larvae indet.	●																			●		●				
Staphylinus (1)																						●				
Stenus (1)	●																									
Tachinus (1)	○						●																			
Tachyporus (5)	●		●				●	○	○	○	●					○			○			●				
Xantholinus (3)	●										●															
DERMAPTERA																										
Forficula (2)	●								○																	
Labidura (1)																●										
DIPTERA																										
Asilidae (1)						●																●				
Cecidomyiidae (2)			●		●																					
Chloropidae (2)				●			●																			
Dolichopodidae (1)						●	●	●							●											
Empididae (6)	●						●	●																		
Muscidae (1)											●															
Sciomyzidae (1)																										●
Scathophagidae (1)	●						●	●			●															
HETEROPTERA																										
Anthocoridae (5)	●		●	○	●	●	●	○										●	●							
Lygaeidae (1)																●										
Miridae (4)	●	○																			●					
Nabidae (5)	●					●	●									●		●		○		●		●		
Pentatomidae (8)							●									●										
Reduviidae (2)																										
Veliidae (1)		●																								
HYMENOPTERA																										
Formica (1)	●					●	●														●					
Formicidae indet.	●										●					●										
Lasius (1)																				●						

(*Continued*)

Table 11.1 (Continued)

PREDATOR TAXON (c. Number of Species)	PESTS																							
	Homoptera							Diptera							Lepid.			Coleoptera						
	Cereal aphids	Rice leafhoppers	Potato aphids	Sugarbeet aphids	Cabbage aphids	Legume aphids	Other Homoptera	Cereal frit fly	Wheat bulb fly	Wheat blossom midges	Cabbage root fly	Carrot fly	Crane flies	Other Diptera	Noctuid moths	Pierid butterflies	Other Lepidoptera	Cereal leaf beetle	Corn rootworm beetle	Colorado potato beetle	Wireworm/Chafer beetles	Other Coleoptera	Sawflies	Slugs & snails
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Myrmica (1)									●															
Pheidole (1)															●									
Solenopsis (1)															●									
ACARI																								
Acari indet.	●																		●					
Pergamasus (1)	●							○																
Trombidiidae indet.	●										●													
Tyrophagus (1)																			●					
ARANEAE: LINYPHIIDAE																								
Bathyphantes (1)	●																							
Erigone (2)	●																							
Lepthyphantes (1)	●																							
Linyphiidae indet.	●																							
Meioneta (1)	●																							
Milleriana (1)	●																							
Monocephalus (1)	●																							
Oedothorax (4)	●	○								○														

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
ARANEAE: LYCOSIDAE																								
Alopecosa (1)	●																							
Lycosidae indet.	●																							
Pardosa (= *Lycosa*) (8)	●	○					○	○	○				●		●									
ARANEAE: OTHERS																								
Araneae indet.		●	●				●							●	●	●								
Araneidae (3)	●	○																						
Clubionidae (1)	●																							
Oxyopidae (2)		○																						
Salticidae (1)		○																						
Tetragnathidae (3)	●	○						○																
Theridiidae (3)	●														●									
Thomisidae (4)		○																	●	●				
OPILIONES																								
Homalenotus (1)	●																							
Leiobunum (2)															●									
Nemastoma (1)	●																							
Phalangida indet.																								●
Phalangium (1)																								
Platybunus (1)	●																							
CHILOPODA																								
Chilopoda indet.																								●
Geophilomorpha indet.																		●						
Lamycetes (1)	●							○																
Lithobius (1)	●							○																
Necrophloeophagus (1)								○																

Data from laboratory feeding tests only (○), otherwise from (or includes) field observations and gut-content analyses of field-collected material (●).

Details of each pest group shown in Table 11.1 (numbered 1–24) and literature sources of predation records:

HOMOPTERA

1. Cereal aphids: *Metopolophium dirhodum* (Wlk.), *M. festucae* (Theo.), *Rhopalosiphum padi* (L.), *Sitobion avenae* (F.) (Aphididae).[6,12,40,41,54,55,78,93,104,105,137,223–230]

2. Rice leafhoppers: *Nephotettix*, *Nilaparvata*, *Recilia*, *Sogatella* spp. (Delphacidae, Jassidae).[58,160,231,232]

(*Continued*)

3. Potato aphids: *Aulacorthum solani* (Kalt.), *Macrosiphum solanifolii* (Ashm.) (= *M. euphorbiae* [Thomas]), *Myzus persicae* (Sulz.) (Aphididae).[94,233–235]

4. Sugarbeet aphids: *Aphis fabae* (Scop.), *Myzus persicae* (Sulz.), *Pemphigus betae* (Doane) (Aphididae).[89,91,94,128,236]

5. Cabbage aphid (on sprouts and other brassicas): *Brevicoryne brassicae* (L.) (Aphididae).[19,237,238]

6. Legume aphids (on alfalfa, clover, cowpea, lucerne and peas): *Acyrthosiphon pisum* (Harris), *Aphis craccivora* (Koch); *Macrosiphum avenae* (F.) (Aphididae).[72,239,240]

7. Other Homoptera: Aphididae indet.; lettuce root aphid, *Pemphigus bursarius* (L.); strawberry aphids, *Pentatrichopus fragaefolii* (Cocker) (= *Capitophorus fragaefolii* (Ckll.), *C. fragariae* (Theo.)) (Aphididae); clover leafhopper (on lucerne*), Aceratagallia sanguinolenta* (Provancher); potato leafhopper (on lucerne), *Empoasca fabae* (Harris) (Jassidae); meadow spital bug (on lucerne), *Philaenus spumarius* (L.) (Cercopidae).[72,94,113,241–244]

DIPTERA

8. Cereal frit fly (all stages): *Oscinella frit* (L.) (Chloropidae).[101,126,148,245,246]

9. Wheat bulb fly (all stages): *Leptohylemyia coarctata* (Fall.) (Anthomyiidae).[146,147,247–250]

10. Wheat blossom midges (larvae): *Contarina tritici* (Kirby), *Sitodiplosis mosellana* (Gehin) (Cecidomyidae).[49,137,251,252]

11. Cabbage root fly (all stages): *Delia radicum* (L.) (= *Erioischia brassicae* [Bouche]) (Anthomyiidae).[2,88,110,253–265]

12. Carrot fly (eggs): *Psila rosae* (F.) (Psilidae).[266,267]

13. Crane flies (larvae): leatherjackets, *Tipula* spp. (Tipulidae).[111]

14. Other Diptera (all stages, but mainly eggs and larvae): clover seed midge, *Contarina* (= *Dasyneura*) *leguminicola* (Lent.); rice gall midge, *Orseolia oryzae* (Wood-Mason) (Cecidomyiidae); onion fly*, Delia antiqua* (Meigen); bean seed flies (pupae*), Delia florilega* (Zett.), *D. platura* (Meig.) (Anthomyiidae); alfalfa (lucerne) leaf miner, *Liriomyza trifoliearum* (Spencer) (Agromyzidae); grass/cereal fly, *Opomyza florum* (F.) (Opomyzidae).[49,54,72,268–270]

LEPIDOPTERA

15. Noctuid moths (Noctuoidea) (eggs, larvae, pupae): black cutworm (on maize), *Agrotis ipsilon* (Hufnagel); turnip moth (on cotton), *Agrotis segetum* (Schiff.); mouse moth (on lucerne), *Amphipyra tragopoginis* (L.); velvet bean cutworm (on soya), *Anticarsia gemmatalis* (Hueb.); red-backed cutworm (on cereals), *Euxoa ochrogaster* (Guenee); cabbage moth (on brussels sprouts), *Mamestra brassicae* (L.); armyworm (on lucerne, maize, grass), *Spodoptera* spp.; cabbage looper (on cole), *Trichoplusia ni* (Hueb.).[72,92,96,106,107,152,153,214,271–277]

16. Pierid butterflies (Papilionoidea, Pieridae) (eggs, larvae): alfalfa (lucerne) butterfly, *Colias eurytheme* ; cabbage white butterflies, *Pieris brassicae* (L.), *P. rapae* (L.); millet butterfly, *Pieris melete* (Papilionoidea).[92,96,150,151,277–279]

17. Other Lepidoptera (eggs, larvae, pupae): groundnut & soya bean leaf miner*, Aproaerema modicella* (Tineoidea); rice stem borer, *Chilo* spp.; rice leaf roller, *Cnaphalocrocis medinalis* (Pyraloidea); sunflower moth, *Cochylis* sp. (Tortricoidea); diamond-back moth (on cole), *Plutella maculipennis* (Curtis) (Tineoidea).[154,160,277,280,281]

(*Continued*)

COLEOPTERA

18. Cereal leaf beetle (eggs): *Oulema melanopus* (L.) (Chrysomelidae).[126,157]

19. Corn rootworm beetle (eggs, larvae): *Diabrotica* spp. (Chrysomelidae).[112,181,185,271]

20. Colorado potato beetle (all stages): *Leptinotarsa decemlineata* (Say) (Chrysomelidae).[155,278,282–286]

21. Wireworm/Chafer beetles (all stages): *Agriotes* and other wireworm species (Elateridae); *Anisoplia segetum* (Herbst); Melolonthinae indet.; Japanese beetle, *Popillia japonica* (Newman) (Scarabaeidae).[108,109,275,278,282,287,288]

22. Other Coleoptera (all stages): alfalfa weevil, *Hypera postica* (Gyllenhal); carrot weevil, *Listronotus oregonensis* (LeConte); bean weevils, *Sitona* spp. (Curculionidae).[72,156,289,290]

HYMENOPTERA (SYMPHYTA)

23. Sawflies (larvae): millet sawfly, *Athalia rosae* (L.); Tenthredinidae indet. (on potato?) (Tenthredinidae).[279,282]

MOLLUSCA

24. Slugs and snails (including eggs): *Arion*, *Deroceras*, *Limax* spp., Limacidae indet., *Tandonia* sp., *Vaginulus* sp. (Pulmonata); *Bradybaena* sp., *Cochlicopa lubricella* (Porro), *Discus* sp., *Euconulus* sp., *Helix aspersa* (Muller) (Gastropoda).[84,241,244, 271,291–303]

which normally hunts prey on the soil surface, may sometimes climb freely on brussels sprout plants, especially in damp conditions, and attack aphids on leaves.[19] Similar plant-climbing behavior by this carabid is reported by Dunning, Baker, and Windley[89] in laboratory tests with sugar beet and by Griffiths[90] in field plots of cereals. Climbing activity on sugar beet plants in the laboratory has been demonstrated for *Harpalus rufipes* and other predominantly ground-dwelling carabids such as *Amara familiaris, Bembidion quadrimaculatum, Bembidion lampros*, and *Trechus quadristriatus*; the two latter species and *Notiophilus biguttatus* have also been recovered from sugar beet foliage in the field.[89,91] Ground-dwelling carabids seen climbing on brussels sprouts in the field include *Harpalus rufipes* and *Trechus quadristriatus*, together with other polyphagous predators such as Anthocoridae, Araneae, and Opiliones.[92] From sweep net samples in cereal crops at different times of day, Vickerman and Sunderland[93] found that some Carabidae (of which *Demetrias atricapillus* was the most numerous), several Staphylinidae (mainly *Tachyporus* and other small species), Cantharidae, the common earwig (*Forficula auricularia*), numerous ground-dwelling Araneae, and some Opiliones frequently climb plants and forage in the crop canopy, especially at night. They also report observations of the carabid, *Bembidion lampros*, climbing plants.

According to Loughridge and Luff,[94] even the large carabid, *Harpalus rufipes*, will sometimes climb cereal plants and eat leaf-feeding aphids, but only above thresholds of temperature and aphid density that may limit its usefulness as a canopy predator in the field. Several other large carabids have also been observed to climb plants in search of prey, e.g., *Pterostichus melanarius* in sugar beet,[89] *Pterostichus cupreus* in cereals,[95] and *Calosoma affine* in lucerne.[96] A detailed account of predator activity on the foliage of lucerne crops in North America is given by Wheeler;[72] species of Anthocoridae, Nabidae, Pentatomidae, Cantharidae, Asilidae, and Dolichopodidae were the most abundant polyphagous predators in the plant canopy; the carabid, *Callida punctata*, was often seen climbing on plants and searching among terminal leaves and into flowers, and workers of *Formica subserica*, usually carrying prey, were observed both on foliage and on the ground. From observations in laboratory arenas and small field cages, Dennis and Sotherton[97] found that the predatory activity of staphylinid beetles, *Tachyporus* spp., when attacking colonies of aphids on wheat plants, caused many aphids to become dislodged and fall to the ground. In these experiments, 9.5% of the aphid population was eaten on the plants, whereas 35% was displaced to the ground. Other studies suggest that up to 90% of a cereal aphid population may fall to the ground each day, encouraged by rainfall, wind, and predator and parasitoid activity.[6,98] Field observations and studies using time-lapse video recording have shown that aphids that become dislodged from plants and drop to the soil often fall prey to ground active predators before they can return to the crop canopy;[90,99,100] this may also apply to other foliar pests, e.g., larvae of frit fly[101] and wheat blossom midges,[49] if forced to move from one plant to another via the soil surface.

Thus, as suggested by Potts and Vickerman,[41] the role of many epigeal predatory arthropods as natural enemies may range between the ground and vegetation zones of crop ecosystems. Much of this movement is by crepuscular and nocturnal species, occurring mainly around dawn and dusk or during the night; the few studies of

nocturnal activity in arable crops[92,93,102,103] suggest that the potential importance of epigeal arthropods as both ground and canopy predators has been largely overlooked or underestimated. However, there is also evidence that the predatory activity of some epigeal species, especially among the larger Carabidae and Staphylinidae, is more or less confined to the soil surface, whereas the activity of other predators, such as most Hemiptera, adult Diptera, and some Araneae, is focused mainly in the vegetation layer.[9,51,72,93,104,105]

Somewhat less is known about the importance of polyphagous predators in the hypogeal habitat, although serological examination of gut contents in field populations of Carabidae and Staphylinidae indicate that adults and larvae of some species may be frequent predators of root-feeding soil pests such as cutworms (Lepidoptera, Noctuidae),[106,107] wireworms (Coleoptera, Elateridae),[108,109] and cabbage root fly (*Delia radicum*)[110] (see Table 11.1). In laboratory arenas, Chapman[111] found that the carabid *Pterostichus melanarius* was able to reduce the numbers of soil-dwelling larvae (leatherjackets) of *Tipula* spp. (Diptera, Tipulidae), possibly by hunting underground using olfactory stimuli. However, direct field observations of predator activity below ground are sparse, apart from the notable study by Brust[112] who used plexiglass plates buried in the soil next to maize plants in order to observe natural predation of corn rootworm, *Diabrotica* spp. (Coleoptera, Chrysomelidae), a serious pest of maize in North America. He found that formicid ants (*Lasius* spp.) and mites (Acari) were significant egg predators in the soil and that larvae of Cantharidae, Carabidae, and Staphylinidae, together with *Lasius* spp. and soil-dwelling centipedes (Geophilomorpha, Chilopoda), all fed on larval stages of the chrysomelid below ground. In addition to these observations, several Carabidae and Staphylinidae and the predatory larvae of some Chloropidae have been found associated with root aphids (*Pemphigus bursarius*) on lettuce,[113] and the staphylinid *Philonthus decorus* is known to burrow into the soil in search of hypogeal prey such as the pupae of winter moth (*Operophtera brumata*).[114] A few epigeal Carabidae (e.g., *Clivina*, *Scarites* spp.) have forelegs modified for digging and other morphological adaptations that reflect a burrowing habit;[86] when abundant, such species may be important predators of the eggs and immature stages of several soil-inhabiting pests (see Table 11.1).

Some carabid beetles and other polyphagous predators of arable fields may also occur in nonarable crops and likewise contribute to the natural enemy complex of these habitats. For example, common "arable" species of *Amara*, *Bembidion, Harpalus, Pterostichus* (Carabidae), *Philonthus* (Staphylinidae), the common earwig (*Forficula auricularia*), and formicid ants (*Formica, Myrmica* spp.) are potential natural enemies of the green apple aphid (*Aphis pomi*), the eggs and larvae of codling moth (*Cydia pomonella*), and the apple maggot (*Rhagoletis pomonella*) in apple orchards.[115–120] Likewise, the common earwig (*F. auricularia*) and species of *Tachyporus* (Staphylinidae), *Anthocoris, Orius,* (Anthocoridae) and *Aphidoletes* (Cecidomyiidae) frequently present in arable crops are recorded as predators of damson-hop aphid (*Phorodon humuli*) in hop plantations.[121–124] The widespread occurrence of some predatory species in diverse arable and nonarable crops is reviewed and emphasized by Potts.[12] Also, there is good evidence that some of these species move from crop to crop and between crops and other habitats.[14,16,17,125,126] Hence, since arable fields often dominate the agricultural landscape and may support a

diverse assemblage of epigeal predatory arthropods, changes in the management of cultivated land that increase field populations of such species, potentially over a large area, may indirectly benefit the natural enemy faunas of other crop habitats within the same agroecosystem and represent a significant step towards the conservation of beneficial organisms in the agricultural landscape as a whole.

11.2.2 Regulation and Suppression of Pest Populations

Polyphagous predators are considered important in the regulation of crop pests because as generalist feeders they can persist in crops during periods when pests are at low density or absent. This means that they can have an effect during critical periods of pest immigration and initial increase by helping to reduce and delay damaging infestations at a time when populations of more specialized predators are often small and insignificant.[7,12,40,41,127,128] Furthermore, the epigeal communities of indigenous polyphagous predators generally found in arable fields include a wide range of taxa that may differ in phenology, population dynamics, microhabitat preference, and feeding behavior. When considered as a single functional unit, the combined activity of different taxa within such communities may span the full annual cycle of crop growth from planting to harvest and over this period impose a succession of mortalities on all or most of the developmental stages of various pests. A diverse community structure and, as pointed out by Newsom,[129] a lack of host specificity are major characteristics that make a complex of polyphagous predators potentially so effective, even though the impact of individual predator species on pest numbers may be quite small or fluctuate between seasons and years.

The impact of predators on pest populations is usually difficult to quantify because prey is often completely devoured, leaving no obvious trace of pest mortality. Nevertheless, attempts have been made to evaluate the effectiveness of natural enemies by direct methods, such as exclusion and augmentation experiments, using barriers and cages in conjunction with traps, insecticides, and controlled release to manipulate predator populations in the field or indirectly from correlations between predator and prey numbers.[130]

The dominant pests of cereals and other annual field crops in cool temperate regions are aphids, and considerable attention has been given to the role of indigenous predators in their control. In particular, the potential value of polyphagous predators in reducing cereal aphid populations early in the season has been studied extensively, ever since Potts and Vickerman[41,131] first showed a significant negative correlation between the numbers of apterous cereal aphids present in samples taken from different fields in southeast England and the proportion of total arthropods that were predatory; they thought that the principal factor affecting peak numbers of aphids was the abundance of (largely) polyphagous predators during the early part of the logistic curve of aphid increase when the density of aphids was low. Similar inverse relationships between numbers of cereal aphids and polyphagous predators are reported by Edwards, Sunderland, and George,[3] Sunderland et al.,[6] and Chiverton.[7] From studies in southwest England, Kendall et al.[132,133] thought that increased activity of polyphagous predators (mainly Carabidae, Staphylinidae, and Araneae) may have contributed to the small number of cereal aphids observed in unplowed

(a)

(b)
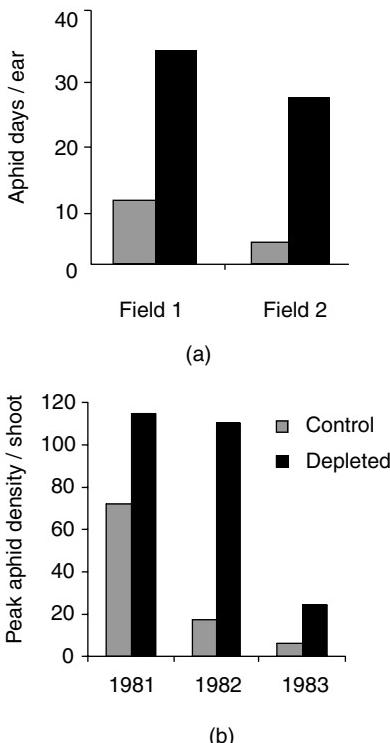
Figure 11.1 Effect of excluding polyphagous predators (from spring onwards) on cereal aphid populations found in July: (a) in plots of winter wheat in two fields in SE England in 1978 (data from Edwards, Sunderland, and George, 1979); (b) in plots of spring barley in Sweden over three consecutive years (data from Chiverton, 1986).

winter barley and wheat crops, resulting in almost complete natural control of aphid-borne barley yellow dwarf virus (BYDV).

Predator-manipulation experiments targeted on aphids in cereal crops have been carried out in Belgium,[39] England,[3,11,134–136] Finland,[10] Germany,[137] and Sweden.[7] Nearly all these studies report much larger aphid populations in predator-depleted plots compared with "control" areas (e.g., up to sevenfold increases where predators were reduced; see Figure 11.1). In most cases, larger aphid populations developed where numbers of polyphagous predators were decreased early in the season (e.g., from spring onwards) than where this was done later (e.g., in summer just prior to ear emergence). Economically damaging infestations of aphids induced by predator reduction are reported from some experiments.[10] More conflicting results were obtained by Holland, Thomas, and Hewitt[138] and Holland and Thomas[11,139] from studies in winter wheat in SE England in 1994–1996, where predator exclusion had no significant effect on aphid density in 2 of the 3 years. This apparent absence of predator impact was attributed to the relatively late arrival and development of aphid infestations in those years combined with warm, dry weather (and possibly other factors) that encouraged aphid increase but reduced the activity of epigeal predators,

especially Carabidae. From these various findings it is now generally accepted that polyphagous predators may often prevent cereal aphid outbreaks by natural regulation and control of aphid populations early in the season but cannot prevent outbreaks in years when climatic and other conditions encourage a rapid increase of aphids late in the season.

Apart from aphids in cereals, there is evidence that epigeal predatory arthropods may help regulate and reduce aphid populations in brussels sprouts,[140] lucerne,[141] peas,[142] potatoes,[143] and sugar beet.[89,128,144,145] From their experiments in the Netherlands to investigate the impact of predatory arthropods on the spread of beet yellows closterovirus (BYV) by the aphid *Myzus persicae*, Landis and van der Werf[128] found that elimination of about 90% of polyphagous predators (mainly Carabidae and Cantharidae) within small barriered plots considerably enhanced the establishment and survival of aphids and increased the spread of BYV by about 50% compared with open sites. They concluded that early predation significantly reduced aphid establishment and subsequent virus spread in this field but were unable to generalize these results in view of the variation in predator populations observed in other suger beet fields.

Less work has been carried out on temperate field crop pests other than aphids. Basedow[49] showed that mortality in a field population of the wheat blossom midge, *Sitodiplosis mosellana*, was greatly increased (84%) by the presence of epigeal predators, of which Carabidae were the most abundant. Various epigeal predators feed on immobile stages, notably eggs and pupae, of root- and shoot-mining Diptera such as onion fly (*Delia antiqua*), cabbage root fly (*Delia radicum*), wheat bulb fly (*Leptohylemyia coarctata*), frit fly (*Oscinella frit*), and carrot fly (*Psila rosae*) (see Table 11.1). Several authors report substantial mortality of egg and pupal stages in field populations of some of these fly pests, thought due mainly to predatory beetles in the soil (Table 11.2). The larval stages feeding within plant tissue are protected and usually escape predation,[146,147] although according to Jones[148] ground predators sometimes bite into grass stems to reach frit fly larvae. Natural control of cabbage

Table 11.2   Reported Predation Mortality of Immature Stages of Root- and Shoot-Mining Diptera Pests Attributed Mainly to Polyphagous Predators

| Pest Species | Mortality (% loss) | | | Reference |
	Eggs	Pupae	All Stages	
Delia radicum (L.)	—	—	90–95	259
(cabbage root fly)	25–50	—	—	1
	47–79	—	—	149
	—	20–30	—	2,262
Leptohylemyia	0	—	—	249
coarctata (Fall.)	50–67	27–34	—	147,250
(wheat bulb fly)	—	5–14*	—	248
	—	15–61	—	250
Psila rosae (F.)	13–60	—	—	267
(carrot fly)				

*Predation by *Aleochara* spp. (Staphylinidae)

(All data from observations and predator exclusion studies in the field).

root fly by polyphagous predators has been shown to reduce damage and yield loss in cauliflower crops.[1,149] Field populations of some Lepidoptera and Coleoptera pests also appear to be limited, in part, by nonspecific arthropod predators. In a 3-year study in England, Dempster[92] found that the natural mortality in each generation of the cabbage white butterfly, *Pieris rapae*, on brussels sprouts, was about 90% between egg and pupal stages; he estimated that over half this mortality (50–60%) was due to arthropod predation on young caterpillars (mainly by Carabidae, Araneae, and Opiliones[150]). Ashby,[151] working in New Zealand, found similar mortality of *P. rapae* larvae (56%) in cabbage crops based on results from predator-exclusion experiments. Predation studies in North America on the fall armyworm, *Spodoptera frugiperda*, in maize[152] and on the velvet bean cutworm, *Anticarsia gemitalis*, in soya[153] have shown that polyphagous predators, such as Carabidae, Forficulidae, and Formicidae, attack pupae of these noctuid moth pests in the soil, causing an annual mortality in the range of 45–95%. Also in North America, Bergmann and Oseto[154] found that larval and pupal populations of the sunflower tortricid moth, *Cochylis hospes*, overwintering in soil, were typically reduced by 40–45% due to predation by Carabidae. The impact of native polyphagous predators on coleopterous pests has only been quantified in a few European studies, such as that of Karg[155] on the Colorado potato beetle, *Leptinotarsa decemlineata* (reporting 5% mortality of larval and adult stages in one field), Hamon, Bardner, and Allen-Williams[156] on the bean weevil, *Sitona lineatus* (claiming that carabid beetles may reduce numbers of larvae and overwintering adults in the soil by more than 30%), and that of Mamedov[157] on the cereal leaf beetle, *Oulema melanopa* (showing that polyphagous predators may destroy about 90% of the eggs and larvae of this pest).

There is some evidence to suggest that indigenous natural enemies may be important in annual field crops of warmer climates. For example, in America there may be as many as 600 species of arthropod predators associated with cotton agroecosystems, with 10–15 families that attack the bollworm and tobacco budworm (*Heliothis* spp.) complex. Although many studies dealing with cotton pest management have stressed the potential value of these predators in natural pest control, there is only limited information on their effectiveness in reducing pest populations below economic densities. Nevertheless, frequent and well documented secondary pest outbreaks following insecticide treatment on cotton are evidence that the natural enemy complex, including polyphagous predators, normally controls many pests.[158] Likewise, in some parts of Asia, rice-stem borers (*Chilo* spp.) may suffer up to 99% mortality from egg to pupal stage in the absence of pesticides, but pest numbers increase when the paddy fields are pesticide-treated.[159] Rice leaf hoppers (*Nephotettix, Nilaparvata, Recilia,* and *Sogatella* spp.) are also controlled by indigenous predators: studies in Japan indicate that a few dominant species from a large guild of spiders (Araneae) could control about 81% of leaf hoppers at their peak abundance, but again chemical control of other rice pests was shown to decrease spider numbers, allowing populations of leaf hoppers to increase.[56,160]

It is evident from these various studies that native epigeal predatory arthropods, when abundant, can help regulate and suppress populations of many crop pests in a wide range of arable ecosystems. Their prime importance is probably as a "buffer" against rapid resurgence of pests, thereby reducing the frequency of serious pest

outbreaks, although there is some documented evidence of polyphagous predators exerting complete natural control over some potential pests. Thus, in the development of farming systems, it is essential to question and establish the likely impact of different cultural options on the epigeal fauna.

11.3 INFLUENCE OF TILLAGE ON PREDATOR ARTHROPODS

For the purpose of this review, the diverse tillage operations used to accomplish soil manipulations are broadly classified as either conventional tillage (CT) by moldboard-type plowing, which completely inverts the soil layers, followed by one or more surface cultivations with rotor, disk, or tine harrows to form a seed-bed, or reduced tillage (RT), which embraces a range of separate mechanical operations using chisels, wing-shares, rotors, disks, tines, and other implements to loosen the soil and form a seedbed but without inverting the soil layers. Reduced tillage also includes the use of specialized, noninversion machines such as the Hoersch- and Dutzi-type cultivators, which combine subsoil and surface tillage and drill the seed in a single-pass operation.[161,162] In all the studies considered here, these systems are compared with no-tillage (NT), which avoids cultivation altogether by direct drilling, where only the seeding coulters cause minor disturbance of the soil surface.

There have been two general approaches to the study of epigeal predatory arthropods in relation to tillage practices. One has focused on measuring abundance (or population activity) and the other has emphasized species diversity. Although undoubtedly linked, each of these aspects is considered separately.

11.3.1 Predator Abundance and Activity in Relation to Tillage

The impact of tillage, or lack of it, on the population activity of epigeal predatory arthropods has been researched in numerous field experiments, mainly in the U.S. and Canada[62,63,66,163–171] and in western Europe.[133,172–174] Most of these investigations show that soil cultivation is typically followed by some decline in the abundance and activity of epigeal predatory arthropods including ground beetles (Carabidae), rove beetles (Staphylinidae), ants (Formicidae), spiders (Araneae), and centipedes (Chilopoda). In some experiments, up to 80% fewer epigeal predators have been recorded after conventional tillage compared with no-tillage, at least during the first few weeks or months after cultivation and crop planting (see Table 11.3). A few studies suggest that the post-cultivation decline of some carabid beetles may last for much of the crop growing season (Figures 11.2 b–c),[62,174] but field populations of most epigeal predatory arthropods generally appear to recover more quickly, often within 3 to 4 months after tillage operations (Figures 11.2 a–d).[62,133,166,167,174] Indeed, over the latter part of the growing season it has frequently been observed that staphylinids (Figure 11.2 c),[174] spiders (Figures 11.2 b and d),[62,133] and some carabids[133] may become increasingly more prevalent on conventional-tillage than on no-tillage plots. These fairly rapid population recoveries from the effects of tillage, particularly among Staphylinidae and Araneae, might be due to the high dispersive powers of many members of these taxa, either by flight (e.g., staphylinids) or aerial

Table 11.3 Reported Effects of Cultivation on the Population Activity of Epigeal Predatory Arthropods

	Crop	Tillage (season)	Ca	St	Fo	Ar	Ch	Tot	Source
(a)	Maize	RT (sp)	+5	—	—	—	—	—	181
		CT (sp)	0	—	—	—	—	—	
(b)	Soybean	CT (sp)	−20	—	—	—	—	—	163
(c)	Grass	CT (sp)	—	—	—	—	−50	—	180
(d)	Sorghum	CT (sp)	−80	—	—	−75	—	—	165
(e)	Maize	CT (sp)	−25	—	—	−20	—	−10	62
(f)	Maize	RT (sp)	−30	—	—	−40	—	−30	166
		CT (sp)	−20	—	—	−20	—	−15	
(g)	Maize	RT (sp)	−10	—	—	+5	—	0	166
		CT (sp)	−15	—	—	+10	—	0	
(h)	Maize	RT (sp)	−15	—	—	0	—	0	166
		CT (sp)	−10	—	—	−35	—	−20	
(i)	Maize	CT (sp)	—	—	—	—	—	−30	167
(j)	Maize	CT (sp)	−55	−30	—	—	—	−45	167
(k)	Maize	CT (sp)	−20	−15	−5	+5*	+5	−15	63
(l)	Wheat	RT (sp)	+10	—	—	—	—	—	170
		CT (sp)	+10	—	—	—	—	—	
(m)	Wheat	RT (sp)	−5	—	—	—	—	—	170
		CT (sp)	−5	—	—	—	—	—	
(n)	Barley	CT (sp)	−10	—	—	—	—	—	171
(o)	Barley	CT (sp)	−25	—	—	—	—	—	171
(p)	Sugar beet	RT (sp)	−30	−15	—	−55	—	—	174
(q)	Sugar beet	RT (sp)	−30	+10	—	−15	—	—	174
(r)	Sugar beet	RT (sp)	−40	+15	—	−30	—	—	174
(s)	Barley	RT (au)	−30	−60	—	−45	—	—	132
		CT (au)	−40	−80	—	−65	—	—	
(t)	Barley	RT (au)	—	—	—	−5	—	—	133
		CT (au)	—	—	—	−30	—	—	
(u)	Wheat	RT (au)	—	—	—	−15	—	—	133
		CT (au)	—	—	—	−70	—	—	
(v)	Wheat	RT (au)	—	—	—	+10	—	—	133
		CT (au)	—	—	—	−10	—	—	
(w)	Wheat	RT (au)	—	—	—	−5	—	—	133
		CT (au)	—	—	—	−20	—	—	
(x)	Wheat	RT (au)	—	—	—	−30	—	—	133
		CT (au)	—	—	—	−60	—	—	
(y)	Soybean	CT (sp)	−5	—	—	—	—	—	66
	Wheat	CT (au)	+5	—	—	—	—	—	

*Only including Lycosidae

Expressed as the percentage difference (D%) in total captures during the first 3–4 months of the growing season on tillage plots (P_t) compared with no-tillage plots (P_n), where $D\% = (P_t − P_n)/(P_t + P_n)*100$ to nearest 5% (RT = reduced tillage, CT = conventional tillage, sp = spring, au = autumn, Ca = carabidae, St = staphylinidae, Fo = formicidae, Ar = araneae, Ch = chilopoda, Tot = all predatory arthropods).
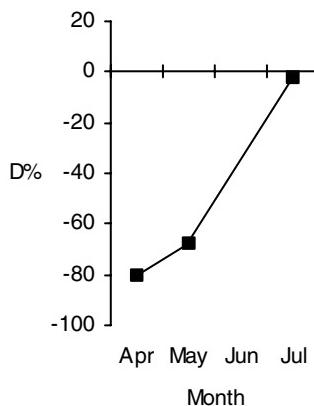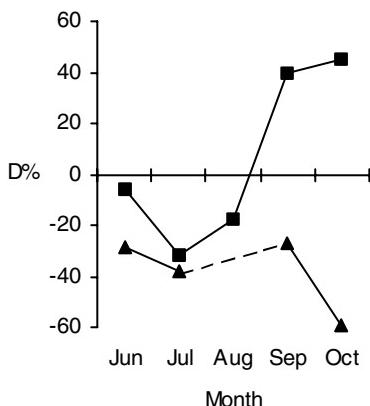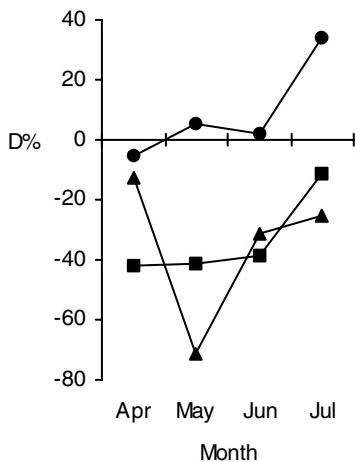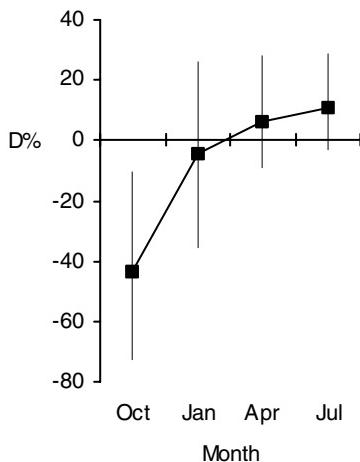
Figure 11.2 Effect of soil cultivation on the population activity of predatory arthropods at different times during the crop-growing season, shown as the percentage difference (D%) in predator numbers caught on tillage plots (P_t) compared with no-tillage plots (P_n), where $D\% = (P_t - P_n)/(P_t + P_n)*100$: (a) in a field of spring-sown maize after conventional tillage in April (data from House and Rosario-Alzgaray, 1989); (b) in a field of spring-sown maize after conventional tillage in May (data from Stinner, Krueger, and McCartney, 1986); (c) in two fields of spring sown sugar beet after reduced tillage in April (average effects over two cropping seasons; data from Heimbach and Garbe, 1996); (d) in two fields of autumn-sown wheat and barley after conventional tillage in September (average and range of effects over three cropping seasons; data from Kendall et al., 1995).

"ballooning" (spiders), although why cultivated plots should be recolonized more than uncultivated as the season progresses is unknown. Kawahara[175] observed rapid recolonization of rice paddies by "ballooning" Linyphiidae soon after crop planting. However, population recovery by dispersal (immigration) is largely dependent on spatial scale, and the duration of effects in relatively small experimental plots may be much shorter than is likely at the larger scale of whole fields, farms, or landscapes.[14,176,177]

Where reduced- and conventional-tillage treatments have been compared in the same experiments, the effects of these cultivations on most groups of predatory arthropods, at least in the early part of the season, tend to increase with increased tillage intensity. In the UK, during the autumn and winter months following September cultivation and planting of cereals (i.e., during September to November and in some years extending up to the end of February), Kendall et al.[133] consistently found most linyphiid spiders in no-tillage plots and fewest in conventional-tillage plots, with reduced tillage intermediate: no-tillage > reduced tillage > conventional tillage (Table 11.3 s–x; Figure 11.3a). Their results for Carabidae and Staphylinidae were less consistent but generally followed the same trend as spiders with respect to tillage intensity, at least during the immediate post-tillage period, September to November (Table 11.3 s).[132] These studies also indicated that reduced tillage with a single-pass Dutzi cultivator had considerably less effect on spider numbers than reduced tillage involving three separate operations with tine-disk cultivators and harrows (Figure 11.3 a). Similar findings related to the number of operations in conventional-tillage systems are reported by Edwards,[178] where plowing with only
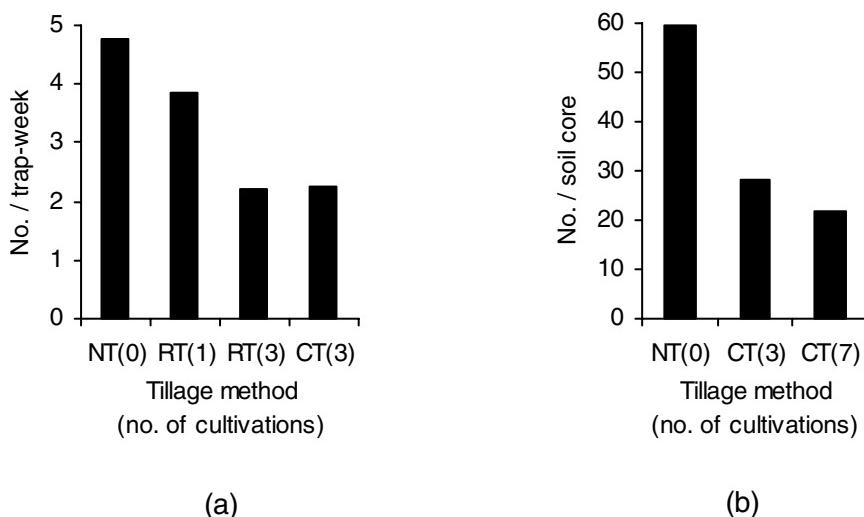
Figure 11.3 Effect of tillage intensity (i.e., the method and number of cultivations; see text for details) on: (a) the population activity of linyphiid spiders (Araneaea, Linyphiidae) during the first 3 months of the growing season in winter wheat (average of three consecutive years; data from Kendall et al., 1995); (b) the abundance of all soil arthropods in reseeded grass (data from Edwards, 1977).

two further "seedbed" cultivations in reseeded grass (least intensive) had less effect on total soil arthropods, including predatory groups, than plowing with six further cultivations (most intensive), although the additional effect of the secondary ("seedbed") cultivations was relatively small compared with the primary influence of plowing (Figure 11.3 b).

Less frequent tillage by annual rotation of conventional- or reduced-tillage methods and no-tillage may also benefit soil arthropods. House[63] observed a twofold increase in the total number of arthropods recovered from soil samples in a wheat–soybean rotation cultivated every second year compared with biannual soil cultivation. The long-term effects of such rotational tillage on predatory arthropods could be worthy of further investigation since it may allow greater flexibility in overall crop management than strict adherence and continuous use of one tillage system.

Timing of operations as well as intensity of cultivation may also be important in determining the impact of tillage on some groups of predatory arthropods. Hance and Gregoire-Wibo[179] found that carabid beetles were affected differently depending on the season in which tillage occurred. Autumn cultivation (plowing) and bare soil over the winter had a greater detrimental effect on numbers of spring-breeding species (adult overwinterers) than autumn breeders (larval overwinterers); it is believed that this is because the latter were mainly present as subterranean larvae and not active on the soil surface over this period. However, in contrast to these observations, Clark, Gage, and Spence[66] and Kendall et al.[133] found no apparent link between the seasonal breeding patterns of these beetles and the effects of spring or autumn cultivation on their population activity. Nevertheless, because many Carabidae, Staphylinidae, and other epigeal predatory arthropods overwinter in field boundaries (i.e., hedgerows, etc.) and have a seasonal migration between boundary habitats and the field,[24,26,28] it does seem very likely that the exact timing of tillage operations in relation to these seasonal movements may determine, at least in part, the impact of cultivation on such species. Thus, policies of early tillage in spring and late tillage in autumn, before and after the main period of field activity, might be useful conservation strategies for some epigeal predators.

There is increasing evidence that some taxa and species of predatory arthropods are more sensitive to cultivation than others or may even display completely opposite reactions to the same cultivation method. In North America, Stinner, Krueger, and McCartney[62] and House and Rosario-Alzgaray[167] found that carabid beetles and some spiders showed a more pronounced decline after conventional tillage in spring maize than did staphylinid beetles and other predatory groups. Similar differences between these taxa in response to reduced tillage are reported by Heimbach and Garbe[174] working in sugar beet crops in western Europe (Table 11.3 p–r; Figure 11.2 c). In another study in spring-sown maize in North America, House[63] found that conventional tillage reduced numbers of Carabidae by 20%, but Staphylinidae by only 15%, while Lycosidae, Formicidae, and Chilopoda were more or less unaffected. Within the Carabidae, species of *Agonum* were unaffected, but numbers of *Harpalus* were reduced by 10%, *Amara* by 30%, and other carabids (mainly *Calosoma* and *Chlaenius* spp.) by about 35%. However, some of these findings are not entirely consistent with other studies. In the UK, Edwards[180] reported that soil populations of centipedes

(Chilopoda) decreased by over 50% after conventional tillage of grassland (cf. House;[63] Table 11.3 c and k). Also, in an experiment in the UK comparing populations of Carabidae, Staphylinidae, and Linyphiidae in cultivated and uncultivated winter barley, Kendall et al.[132] showed that a guild of larger staphylinids present during autumn (i.e., *Philonthus*, *Quedius*, *Staphylinus,* and *Xantholinus* spp.) seemed to be more sensitive to tillage operations than the dominant carabids (i.e., *Bembidion*, *Nebria*, *Pterostichus,* and *Trechus* spp.) and linyphiid spiders found at this time (cf. Heimbach and Garbe;[174] Table 11.3 s and p–r). Further studies of the relative abundance of 23 generic groups of Carabidae and Staphylinidae in two tillage experiments in winter cereals over a period of 3 years indicated that while some carabids, e.g., species of *Calathus*, *Carabus*, *Notiophilus,* and *Pterostichus*, and staphylinids, such as *Lathrobium*, *Quedius*, *Staphylinus,* and *Tachinus* spp., were to varying degrees consistently favored by reduced- or no-tillage treatments, other carabids, e.g., *Bembidion*, *Clivina*, *Demetrias,* and *Trechus* spp., and staphylinids belonging to the genus *Tachyporus* were typically more frequent in conventionally-tilled plots. Several taxa seemed largely unaffected by tillage or had inconsistent distributions between experiments and years; these included species of *Abax*, *Agonum*, *Asaphidion*, *Harpalus*, *Loricera,* and *Nebria* (Carabidae); *Oxytelus*, *Philonthus*, *Stenus,* and *Xantholinus* (Staphylinidae), although *Abax*, *Agonum*, *Harpalus,* and *Philonthus* spp. usually tended to be slightly more prevalent in no-tillage plots.[133]

Different effects of tillage on different species of Carabidae have been reported from other experiments, mainly in the U.S. and Canada.[66,170,171,181,182] In all these studies, individual species of dominant carabids reacted in more or less opposite ways to soil cultivation, resulting in little or no overall difference in their combined density, i.e., at the family level, between conventional- and no-tillage treatments (see Table 11.3 a, g, l, m, and y). For example, in an experiment over two years comparing conventional- and no-tillage systems in a spring soybean and winter wheat rotation, Clark, Gage, and Spence[66] found four common carabids—*Pterostichus melanarius*, *P. lucublandus*, *Cyclotrachelus sodalis,* and *Agonum placidum*—that together represented nearly 90% of the total carabids caught in the experimental plots. Two of these species, *P. melanarius* and *P. lucublandus*, were more or less unaffected by cultivation, whereas numbers of *C. sodalis* were significantly reduced by about 50% under conventional tillage compared with no-tillage, but this was largely offset by increased numbers of *A. placidum* in the conventionally-tilled plots. Hence, these four species were representative of all possible types of reaction to the same tillage treatments.

The conflicting effects of tillage on different species of Carabidae and Staphylinidae found in these and other studies are broadly summarized in Table 11.4. Similar opposite responses to cultivation intensity amongst different species of spiders are reported by Kleinhenz and Buchs.[183] These observations suggest it is unwise to treat large taxonomic groups as single entities. Conclusions based on combined species data, certainly in Carabidae and Staphylinidae, and probably in other taxa at the level of order, family, or even genus, are not easily generalized without some knowledge of species composition and behavior. Differences in species dominance from one study to another may well give rise to apparent anomalies in experimental findings. Much of the variability in the results summarized in Table 11.3, for example, may reflect this point.

Table 11.4 Reported Prevalence of Different Species of Carabidae and Staphylinidae in No-Tillage (NT) or Reduced Tillage (RT) and Conventional Tillage (CT)

More Prevalent in NT, RT	More Prevalent in CT	No Difference or Inconsistent
CARABIDAE:	CARABIDAE:	CARABIDAE:
Agonum cupreum (Dej.)	*Agonum placidum* (Say)	*Abax parallelepipedus* (Pill.)
A. muelleri (Herbst)	*Amara lacustris* (Lec.)	*Agonum dorsale* (Pont.)
A. punctiforme (Say)	*A. latior* (Kirby)	*Amara torrida* (Panz.)
Amara carinata (Lec.)	*A. quenseli* (Schon.)	*Anisodactylis ovularis* (Csy.)
A. obesa (Say)	*Apristus subsulcatus* (Dej.)	*Asaphidion flavipes* (L.)
Anisodactylis merula (Ger.)	*Bembidion aeneum* (Ger.)	*Bembidion lampros* (Herbst)
Bembidion bimaculatum (Kirby)	*B. guttula* (F.)	*B. obtusum* (Serv.)
B. rupicola (Kirby)	*B. lunulatum* (Four.)	*Bembidion 4-maculatum* (L.)
Calathus fuscipes (Goeze)	*B. tetracolum* (Say)	*B. 4-maculatum oppositum* (Say)
Calosoma alternans sayi (Dej.)	*Cicindela* sp.	*Calosoma calidum* (F.)
Carabus monilis (F.)	*Clivina fossor* (L.)	*Harpalus fallax* (Lec.)
C. nemoralis (Mull.)	*Cratacanthus dubius* (Beau.)	*H. pensylvanicus* (Deg.,)
C. violaceus (L.)	*Demetrias atricapillus* (L.)	*H. rufipes* (Deg.,)
Chlaenius tomentosus (Say)	*Megacephala carolina* (L.)	*Loricera pilicornis* (F.)
Cyclotrachelus sodalis (Lec.)	*Pterostichus chalcites* (Say)	*Nebria brevicollis* (F.)
Harpalus affinis (Schr.)	*P. scitulus* (Lec.)	*Pterostichus lucublandus* (Say)
H. caliginosus (F.)	*Trechus quadristriatus* (Schr.)	*P. melanarius* (Ill.)
Megacephala viginica (L.)		*Trechus apicalis* (Mts.)
Notiophilus spp.		
Pterostichus adstrictus (Esch.)		
P. cupreus (L.)		
P. madidus (F.)		
P. niger (Schal.)		
P. strenuus (Panz.)		
P. vernalis (Panz.)		
Scarites subterraneus (F.)		
Selenophorus opalinus (Lec.)		
Tachys sp.		
STAPHYLINIDAE:	STAPHYLINIDAE:	STAPHYLINIDAE:
Lathrobium spp.	*Tachyporus* spp.	*Philonthus* spp.
Quedius spp.		*Xantholinus* spp.
Staphylinus spp.		
Tachinus spp.		

Source: From References 66, 133, 163, 170, 171, 181, 182, 192, 300, 304.

Long-term studies in Germany have shown that conventional tillage is detrimental not only to many epigeal macroarthropods grouped as polyphagous predators but also to soil microarthropods, including predatory mites (Mesostigmata, Gamasina, etc.), and to other beneficial antagonists such as hymenopterous parasites.[184] Significantly fewer

predatory mites have also been reported under conventional tillage compared with reduced or no-tillage in the UK[178] and North America.[161,165,166,185,186]

Although tillage might be expected to have the greatest impact on soil- and soil-surface-dwelling arthropods, it also appears to influence the abundance and distribution of predatory foliage-inhabiting insects. Conventionally tilled soybeans have generally been found to support far fewer of these insects, especially predacious Hemiptera, than no-tillage systems.[164,187,188] The greater abundance of foliage-inhabiting predators under no-tillage has been attributed in part to increased weed density resulting from no-tillage[164] or to complex interactions between the tillage system, crop planting date, row spacing, and previous crop stubble.[187] On the other hand, Troxclair and Boethel[188] concluded that weed density and species were not significant factors affecting foliage-inhabiting insects in their study.

11.3.2 Species Diversity of Predators in Relation to Tillage

The impact of tillage on species diversity within epigeal communities of predatory arthropods has received relatively little attention compared with the number of studies on population-activity effects. In North America, Blumberg and Crossley[189] compared pitfall trap captures of all soil surface arthropods in conventional-tillage and no-tillage sorghum and an adjacent old field. Total numbers of individuals and species captured were greater in no-tillage (ca. 267 individuals of 89 species) than either conventional-tillage (ca. 179 individuals of 63 species) or the old field (ca. 198 individuals of 70 species). The Shannon index of general diversity[190] for no-tillage was consistently higher than for conventional tillage throughout the crop-growing season (June–December; Figure 11.4 a). The complex of arthropods captured under no-tillage was composed of relatively more individuals and species of predators and parasites than under conventional tillage. Percentages of individuals and species represented by spiders, for example, were similar in no-tillage (30% and 15%) and the old field (22% and 17%) but substantially less in conventional tillage (11% and 8%, respectively). Crop leaf area removed by grazing insects was less in no-tillage (12%) than in conventional tillage (28%). They concluded that the overall increase in arthropod abundance and diversity in no-tillage, and the decrease in herbivory, was indicative of greater stability within this system relative to conventional tillage.

House and Rosario-Alzgaray,[167] working in maize, likewise found that the overall diversity of soil arthropod species (as indicated by the Shannon index) was greater in no-tillage than conventional tillage, but only during the early part of the crop-growing season (April–May). No difference was found between tillage systems after midseason (June; Figure 11.4 b). In an earlier study, House and All (1981) reported more species of Carabidae in soybeans under no-tillage (22 species) compared with conventional tillage (19 species). This difference in species richness persisted throughout most of the growth and maturation stages of the crop.

Weiss et al.,[170] again in North America, examined the similarity in carabid fauna of spring wheat under different tillage and cropping systems (using the Sorenson index of similarity).[191] They generally found greater similarity between the carabid communities of no-tillage and reduced-tillage plots than between either of these and

conventional-tillage plots. However, the highest index values were always associated with similar cropping systems (continuous cropping and each phase of an annual crop–fallow rotation) rather than similar tillage systems, suggesting that cropping system may be more important than tillage in determining similar carabid fauna.

In Belgium, Baguette and Hance[192] investigated the carabid fauna of four crop types (winter wheat, winter barley, spring maize, and spring sugar beet) established by conventional tillage, either with deep plowing (30 cm) or shallow plowing (15 cm), and by no-tillage. With the exception of winter barley, the Shannon index of general diversity increased as tillage intensity decreased (Figure 11.4 c), mainly because the less abundant carabid species in deep plowing became more numerous under shallow plowing or no cultivation. Species richness appeared to depend more on crop type.

Carcamo,[182] working in Canada, noted a trend towards more carabid species in spring barley under reduced compared with conventional tillage, although the
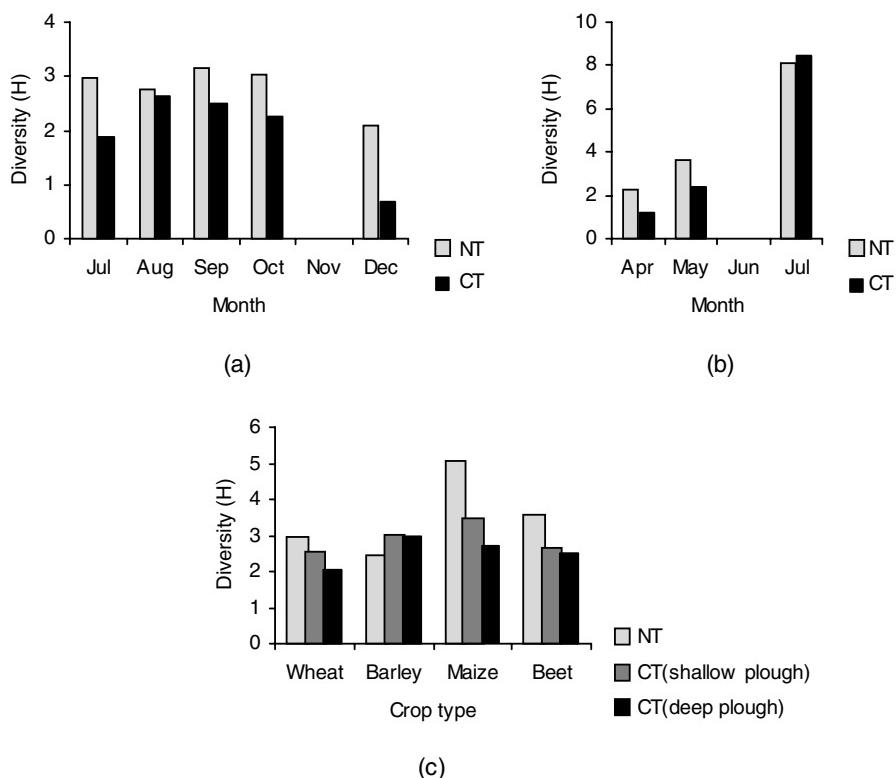
Figure 11.4 Effect of soil cultivation on the species diversity of epigeal arthropods measured by the Shannon index of general diversity (H) for: (a) total arthropod species in sorghum at different times of the crop growing season (data from Blumberg and Crossley, 1983); (b) total arthropod species in maize at different times of the crop growing season (data redrawn from House & Rosario-Alzgaray, 1989); (c) Carabidae captured from April until crop harvest in winter wheat, winter barley, spring maize, and spring sugar beet (data from Baguette and Hance, 1997).

difference was only of marginal significance (10–12 species per trap in reduced tillage vs. 8–10 species per trap in conventional tillage). Nevertheless, there was a highly significant increase in the Shannon index of diversity in the reduced-tillage system (ca. 1.6–2.0 in reduced tillage vs. 1.1–1.3 in conventional tillage). However, in another experiment with spring barley, Carcamo, Niemela, and Spence[171] found no difference in carabid diversity associated with tillage regimes (none vs. conventional). These contradictory results were attributed in part to the dominance of the exotic species *Pterostichus melanarius* in the latter experiment and possible interspecific competition between this introduced carabid and native species.

11.3.3 Mechanisms of Tillage Effects on Predator Abundance and Diversity

The primary mechanisms thought to be involved in determining the impact of tillage on the activity, population dynamics, and diversity of epigeal predatory arthropods and other soil invertebrates in agroecosystems, either directly or indirectly, are summarized in Figure 11.5.

Direct effects of tillage seem most likely in those species that remain in arable fields throughout much of the year to breed, develop, or hibernate. Many field-inhabiting species may be able to withstand some degree of soil disturbance, but certain life stages are likely to be more vulnerable (e.g., less mobile larvae, pupae, estivating or hibernating adults, etc.), and direct mortality may occur due to physical injury, desiccation caused by sudden changes in abiotic conditions, e.g., humidity and temperature,[193] or exposure to increased predation, e.g., by birds and small mammals.[13,180]
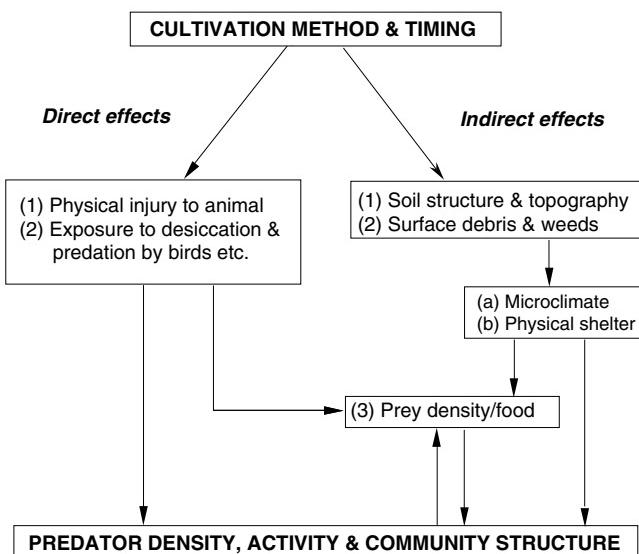
Figure 11.5 Mechanistic effects of soil tillage that may directly or indirectly affect the activity, abundance, and diversity of epigeal predatory arthropods (see text).

Indirect effects of tillage on epigeal predatory arthropods seem broadly associated with three main factors: soil structure, ground cover, and prey density. Effects of cultivation on the structure of the soil top layer and soil surface may impinge on the movement, dispersal, and prey-searching efficiency of some predator species or indirectly affect the amount of physical shelter or places to settle; for example, the number of suitable web-building sites seems to have an important influence on the density of some linyphiid spiders.[194]

Soil cultivation may modify the weed flora of arable fields due to redistribution of weed seeds in the soil[195] and thus give rise to further indirect effects on predatory fauna. Weedy ground cover has been shown to increase the abundance and activity of some carabid and staphylinid beetles[45,196,197] and spiders.[9,198] In North America, House[63] observed that total soil arthropod density was consistently higher in weedy, no-tillage treatments than in other combinations of tillage and weed management: no-tillage without herbicides > no-tillage with herbicides > conventional tillage without herbicides > conventional tillage with herbicides. However, in this study, epigeal predatory arthropods, especially Carabidae, were most abundant in no-tillage with herbicides, believed to be due to the selective increased survival of certain favorable weed species under this particular management regime. In a review of no-tillage experiments in the tropics, Rijn[199] also indicated that crop stubble as well as weeds contributed to the maintenance of predator populations. The increased amounts of stubble and plant residue generally left on the soil surface in reduced- and no-tillage systems[195,200] appear to encourage the winter survival of some adult spring-breeding Carabidae.[179]

It is well known that cultivation can significantly reduce the numbers of earthworms (Lumbricidae), springtails (Collembola), mites (Acari), and other small invertebrates living in or on the soil.[161,165,166,180,200–203] These animals are important alternative prey of many polyphagous predators,[78,81–83] and depletion of such food resources through tillage may indirectly cause decline in predator populations. Furthermore, Hokkanen and Holopainen,[204] Carcamo, Niemela, and Spence,[171] and Kendall et al.[133] suggested that species interactions among predators themselves could be responsible for some of the patterns they observed. Epigeal predatory arthropods may prey upon one another, causing differences in relative abundance and distribution.[13,205] This is an interesting hypothesis, discussed at some length by Carcamo, Niemela, and Spence,[171] and perhaps should be further investigated since it could result in counterproductive measures of predator enhancement. It could also explain some of the contradictory results reported in the literature.

11.4 TILLAGE IN RELATION TO OTHER AGRONOMIC PRACTICES

While tillage has a major influence on the abundance and diversity of predatory arthropods, research has demonstrated that it also interacts significantly with other agronomic practices to affect changes in the fauna of agroecosystems. Specific cultural practices thought to interact with tillage in this way include mulching, weed management, undersowing, spatial planting patterns, cover cropping, and crop rotation.[13,161] Space prevents a detailed review here, but there is sufficient evidence

to conclude that effects of tillage on predatory fauna cannot be generalized over different cropping systems and that the outcome of changing or modifying tillage practice on predator assemblages will depend both on the biological traits of particular species and on the combination of other agronomic treatments applied.[66,170,171] In general, however, the ecological processes that lead to the observed effects of different cultural practices and interactions on predatory fauna remain unclear. Weed management is perhaps the most extensively researched topic, other than tillage, with respect to epigeal fauna and several studies have explored the use of weeds in the manipulation of beneficial insects.[206–211] But even here, the complex interactions of selective weed management in different tillage systems and the ecology of predatory fauna are only poorly understood and warrant further study.[63]

Tillage may also interact with pesticide use to influence the side effects that some of these chemicals have on beneficial organisms. Epigeal predatory fauna are particularly sensitive both to soil-applied pesticides and to fallout from foliar sprays.[212,213] Investigating chemical control of cutworm pests in maize, Brust, Stinner, and McCartney[214] found that a soil-applied organophosphate insecticide suppressed the activity of epigeal predatory arthropods more in no-tillage than in conventional-tillage plots, possibly because predator activity was more concentrated near the soil surface of the no-tillage system. In a review of conservation-tillage agriculture, Stinner and House[161] concluded that many pesticides have nontarget effects that may interact with tillage systems to change the net impact of invertebrates at nearly every trophic level in the agroecosystem, e.g., as pests, natural enemies, and decomposers.

11.5 CONCLUSIONS

The native epigeal predatory arthropods (polyphagous predators) commonly associated with agroecosystems are known to feed on a wide variety of important crop pests, and when abundant they can help regulate and suppress pest populations. Changes and developments in cultural practices that encourage these natural enemies form the base of integrated pest management in the development of sustainable, less intensive agricultural systems. Together with other cultural practices such as cropping patterns and agrochemical use, tillage ranks as a strong determinant of arthropod distribution and abundance.

There is little doubt that the impact of cultivation on epigeal predatory arthropods strongly depends on the intensity of soil tillage. Tillage method, the number of operations, and the frequency of soil cultivation may all have some impact.[63,133,178] The timing of tillage operations in relation to species phenology and behavior may also be important.[179,215] In general, both the abundance and diversity of soil fauna tend to increase as tillage intensity is reduced.

However, individual species often differ in their response to soil disturbance, and even opposite reactions to the same tillage method can be recognized. Such effects are probably related to different ecological requirements depending on species size, larval life cycle, food, etc.[192] Opposite effects at the species level can result in

no effects being recorded at a genus, family, or higher taxonomic level. Such opposite reactions to soil tillage and other crop-management practices have been found among different species of Carabidae, Staphylinidae, Araneae, and other taxa of predatory arthropods.[66,133,170,171,181–183,192,196,197,216] These observations demonstrate the importance of taxonomic level in identifying the full effects of different agronomic practices. As a general rule, it appears essential to work at the species level. Thus, with respect to large taxonomic groups, measurement of species diversity, a function of both the number of species (species richness) and their relative frequency (dominance), is probably a better indicator of the overall significance of treatment effects than total abundance alone. This can also be argued from a theoretical standpoint, since ecological dogma, though not resolved regarding cause and effect, couples the properties of diversity and stability, and diversity within agroecosystems has been used as an indicator of relative stability.[217] With regard to natural pest control and pest management, there is considerable support for the concept that farming practices that increase the diversity of natural enemies and, hence, the trophic complexity of an agroecosystem should lead to greater long-term stability and more easily sustained productivity.[218,219] Thus, as a general principle, the potential use of soil tillage, or indeed any other cultural practice, to promote reliable and sustained biological control of crop pests by native predatory arthropods is perhaps best evaluated primarily from impact on predator diversity, with effects on overall predator abundance given only secondary consideration.

Soil tillage is thought to exert direct and indirect effects on the activity, population dynamics, and diversity of epigeal fauna (see Figure 11.5). Variable interactions between the different biotic and abiotic factors that appear to be influenced by soil tillage, combined with differences in species response (as outlined above), could explain many of the conflicting results observed in field experiments (e.g., Table 11.3). As pointed out by Carcamo, Niemela, and Spence,[171] unraveling the various ecological processes that lead to the observed responses of fauna to different tillage practices requires an experimental approach in which biological interactions are tested and environmental variables are manipulated and measured in more detail. Furthermore, "community" effects (including those observed for large taxonomic groups) represent a composite picture, reflecting the individual biological traits of particular species; thus, the effects of tillage, and indeed other agronomic practices, are expected to vary across faunal assemblages.

There are no methods of soil tillage that comply with all the objectives of the European Commission guidelines on "Good Agricultural Practice."[220] However, some general principles can be identified from the results of field investigation. In general, soil tillage must be reduced in intensity and frequency, and the development of integrated farming systems should aim towards the longest periods of nondisturbance (i.e., no-tillage). For some soil types and cropping systems, or due to peculiar, localized weed and pest problems, it may be impractical to adopt no-tillage or even reduced-tillage systems. Nevertheless, under the broad umbrellas of both conventional and reduced tillage are various options and strategies that can be adopted to minimize soil disturbance and reduce impact on beneficial fauna. These are summarized below, more or less in descending order from most intensive to least intensive:

Conventional tillage (most intensive)

> Minimize plowing depth, e.g., no more than 15 cm deep.[192]
>
> Minimize the number of operations, e.g., no more than two or three seedbed cultivations after plowing.[178]
>
> Reduce the frequency of use by tillage rotation, i.e., maximize the use of reduced tillage and no-tillage in a fixed or flexible rotation with conventional tillage.[63]

Reduced tillage

> Minimize the number of operations, e.g., by using a single pass, combine cultivator drill for crop establishment.[133]
>
> Reduce the frequency of use by tillage rotation, i.e., maximize the use of no-tillage in a fixed or flexible rotation with reduced tillage.[63]

No-tillage (least intensive)

> Continuous no-tillage (direct-drilling)

All tillage systems

> Adjust the timing of operations to avoid the main summer activity period of epigeal predatory arthropods, i.e., as far as possible confine tillage (and drilling) operations to early spring or late autumn.

There is ample evidence that farming systems that eliminate or reduce synthetic fertilizers and pesticides and use crop rotation, cover crops, undersowing, and manures tend to promote the overall abundance of predatory arthropods as well as other natural enemies.[13,50,161,171,220–222] Selective weed management may also encourage some predatory fauna and beneficial insect parasites.[63,196,208] The combined effects and interactions of these agronomic factors and soil tillage on native predatory arthropods and other natural enemies suggest that changes in tillage practice aimed at biological control and integrated pest management must be considered in the context of the whole farming system. Nevertheless, reduced intensity of tillage must be regarded as a key factor of pest management for low-input agricultural systems, if for no other reason than being the first major cultural activity of crop establishment.

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